1   Reefal ostracod assemblages from the Zanzibar Archipelago (Tanzania)

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13

14   **Abstract**

15   Tropical reefs encompass tremendous biodiversity yet are imperiled by increasing
16   natural and anthropogenic disturbances worldwide. Meiobenthic biotas on coral reefs,
17   for example, ostracods, may experience substantial diversity loss and compositional
18   changes even before being examined. In this study, we investigated the reefal ostracod
19   assemblages from the highly diverse and productive ecosystem in Zanzibar
20   Archipelago (Pemba, Zanzibar, and Mafia islands), Tanzania, to understand how their
21   diversity and faunal structure vary in response to water depth, benthic community type,
22   and human impacts. We characterized four distinct ostracod faunas associated with
23   different benthic habitats, which were deep fore reefs, shallow fringing reefs, degraded
24   fringing reefs, and algal covered intertidal flats. We identified typical ostracod
25   associations, i.e., Bairdiidae versus Loxoconchidae-Xestoleberididae, that showed
26   affinities to hard corals or algae on the reef platforms, respectively. Highest diversity
27   was found on shallow fringing reefs where reefal and algal taxa exhibited maximum
28   overlap of their distributional ranges, while the sand flats, mangrove, and marginal reefs
29   within the intertidal zone had much lower diversity with high dominance of euryhaline
30   taxa. Along the western coast of Zanzibar, coastal development likely resulted in a
31   unique faunal composition and comparatively low diversity of ostracod assemblages
32   among those in reefal habitats, in conjunction with overall reef ecosystem degradation.
33   This study represents the first large-scale assessment of shallow-marine ostracods in

34   the Zanzibar Archipelago. It lays a solid foundation for future research into the

35   ecological significance of ostracods on coral reefs.

36

37   **1 Introduction**

38   Coral reefs as the most diverse ecosystem in the marine realm hold great ecological and

39   economic values, yet our knowledge of its enormous biodiversity is far from complete.

40   Compared with well-studied, conspicuous macrofauna (Souza et al., 2023), meiofauna

41   on coral reefs are highly under-represented in current research despite being

42   ecologically essential components and contributing significantly to total biodiversity

43   (Leray and Knowlton, 2015; Plaisance et al., 2011). Ostracoda (Crustacea) among all

44   meio-benthos has a tight association with reef environments tracing back to the lower

45   Paleozoic (Whatley and Watson, 1988). As a useful model organism in modern and

46   paleo biodiversity research because of its high fossilization potential, high abundance,

47   and ubiquity in almost all marine ecosystems (Yasuhara et al., 2017), does ostracod

48   exhibit higher diversity in reefal habitats compared with other soft sediment

49   environments? What are the characteristic ostracod taxa occupying different niches on

50   coral reefs? Answers to these questions are important for a holistic understanding of

51   the reef ecosystem and may hint at the underlying mechanisms that support such

52   extraordinary reef diversity. With intensifying anthropogenic disturbances at local to

53   global scales, the need to examine reefal ostracods before they perish is pressing.

54

55   Studies targeting tropical shallow-marine ostracods on coral reefs are surprisingly

56   deficient. Across the circumtropical belt, the central Indo-Pacific receives the most

57   attention for its diverse reefal ostracods, with pioneering studies identifying distinct

58   faunas associated with depth habitats from the shallow intertidal to deep reefal zones

59   (Whatley and Watson, 1988; Babinot and Degaugue-Michalski, 1996). Apart from

60   bathymetry, the distribution of reefal ostracods seems also related to benthic

61   community type (coral reefs versus seagrass/algal beds), sediment type (i.e., sandy

62   versus muddy deposits), in addition to local hydrology (i.e., exposure to wave energy)

63   (Weissleader et al., 1989; Whatley and Watson, 1988; Babinot and Degaugue-

64   Michalski, 1996; Tabuki, 1990, 1987). However, most of these works are confined to

65   small geographic areas and based on limited (sub)fossil materials. An extensive

66   regional-scale survey of reefal ostracods has never been conducted. More importantly,

67   the focus of previous studies mainly revolved around taxonomy, and biogeography to

68 a lesser degree, while quantitative assessments of biodiversity are largely lacking

69 (Tabuki, 1987, 1990; Mostafawi et al., 2005). The highest species richness (S=74) was

70 reported for a reef slope environment in Pulau Seribu, Java (Whatley and Watson, 1988)

71 in contrast to much lower values at lagoons (S=27-42) (Babinot and Degaugue-

72 Michalski, 1996; Weissleader et al., 1989) and reef flat (S=34) (Mostafawi et al., 2005).

73

74 Reefal ostracods are even less known in other tropical regions outside of the central

75 Indo-Pacific. Along the eastern coast of Africa, where the reef ecosystem is productive

76 and biodiverse, the only studies on ostracod assemblages are perhaps Hartmann (1974)

77 and Jellinek (1993) that document more than 200 species inhabiting the algae facies

78 and reefal facies across the littoral zone in Kenya. Here we present the first large-scale

79 study on reefal ostracods from the Zanzibar Archipelago, Tanzania, a biodiversity

80 hotspot of great conservation interests and vulnerability to increasing anthropogenic

81 impacts (Grimsditch et al., 2009). We investigated the geographical structure of

82 ostracod diversity and composition in relation to environmental habitats among three

83 major islands of Pemba, Zanzibar, and Mafia. We compared the patterns with those of

84 benthic foraminifera (Thissen and Langer, 2017) to explore complex environmental

85 controls on the two groups of meio-benthos. This study is a major step towards better

86 understanding of tropical shallow-marine ostracods in eastern Africa and provides

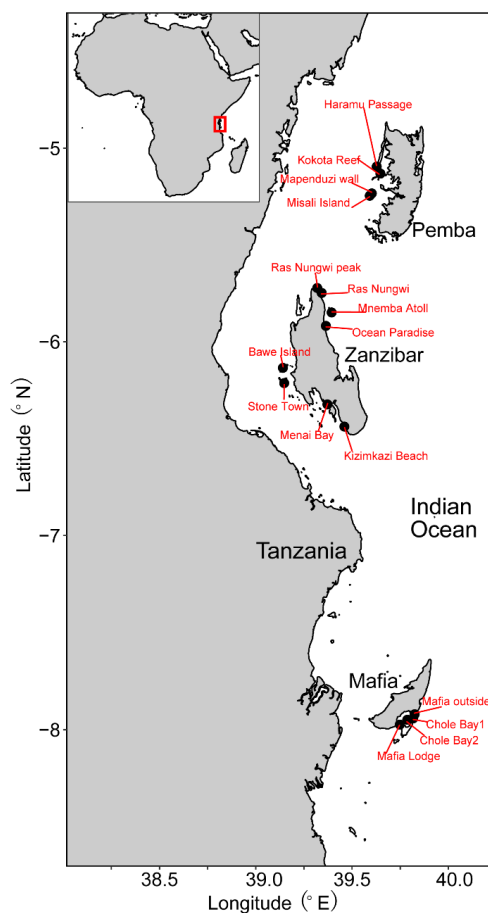87 valuable insight into the ostracod-reef association in general.

88

89 **2 Regional setting**

90 The Zanzibar Archipelago is located along the eastern coast of Tanzania in the Western

91 Indian Ocean (Fig. 1) (Thissen and Langer, 2017). It belongs to the eastern African

92 biogeographic province that stretches from Somalia to the northeastern coast of South

93 Africa (Costello et al., 2017; Obura, 2012). The archipelago is strongly influenced by

94 the warm, westward-flowing South Equatorial Current and the northward-flowing East

95 African Coastal Current (Narayan et al., 2022). The western coastlines are more

96 protected, with generally higher coral coverage, whereas the eastern coastlines are

97 exposed to large physical disturbances and strong wave energy (Thissen and Langer,

98 2017). Tides there are semi-diurnal, with a maximum range of 4.5 m and a neap tidal

99 range of 0.9 m (Thissen and Langer, 2017; Narayan et al., 2022). The islands possess a

100 great variety of benthic habitats from the littoral to open-water zone, with mangroves,

101 vegetated sand flats, and reef complexes. Reefs are mainly fringing reefs that are

102   situated on the narrow continental shelf (Mafia, Zanzibar) or are separated from the

103   African mainland by the deep Pemba channel (Pemba) (Thissen and Langer, 2017).

104   Noticeably, the major islands are subject to very different degrees of human exploration,

105   as Zanzibar is densely populated and highly urbanized while Mafia and Pemba are

106   largely uninhabited (Narayan et al., 2022). Stone Town and Bawe, in particular, are

107   faced with a direct discharge of untreated domestic sewage along the western coast of

108   Zanzibar Island, where moderate levels of reef deterioration have been found with

109   diversity decrease and coral cover loss (Bravo et al., 2021; Larsen et al., 2023).

110   Although extensive long-term monitoring is still lacking, previous studies indicate that

111   Pemba reefs are likely in pristine conditions with the highest coverage of live hard

112   corals, while Zanzibar reefs are often dominated by dead corals intermingled with algae

113   and seagrass habitats (Ussi et al., 2019; Larsen et al., 2023; Grimsditch et al., 2009).

114   No quantitative assessment of reef health has been conducted in Mafia Island,

115   unfortunately, but our field observations suggested moderate to good conditions at our

116   sampling sites.

Fig. 1. Locality map showing three major islands of the Zanzibar Archipelago with sample sites.

3 Materials and methods

3.1 Samples

26 surface sediment samples were collected from 16 sites during two field campaigns in 2005 at the islands of Zanzibar and Pemba, and in 2012 at Mafia Island (Table 1). Depositional depths of all samples range from 0 to 42 m across the intertidal and subtidal zones. The selected sampling sites cover all major types of benthic habitats, including nearshore mangroves, coastal sand flats, and fringing-, fore-, and back-reefs. Samples were collected by SCUBA diving to fill plastic bags with surface sediments from the top 2 cm.

131   Most sampling sites were fine to medium-grained carbonate-rich, bioclastic sands and
132   deposits with some reef rubble. Sediments were washed through a 63 μm sieve and
133   oven dried at 50 °C. The residue was dry sieved over a 150 μm mesh sieve and ostracods
134   were picked from the >150 μm size fraction, because smaller individuals are usually
135   early juveniles that are not preserved and/or difficult to identify (Yasuhara et al., 2017).
136   Sediment-rich samples were split into aliquot fractions using a microsplitter. The
137   sample materials were primarily death assemblages though a small number of
138   specimens were preserved with soft parts, indicating they were alive at the time of
139   collection. Both live and dead specimens were included in the total count to represent
140   time-averaged assemblages, which method effectively defines reef habitats and
141   provides general environmental and diversity data useful in paleoecology (Glenn-
142   Sullivan and Evans, 2001; Langer and Lipps, 2003). A single valve or a carapace was
143   considered as one individual, which is a standard counting method in ostracod research
144   (Yasuhara et al., 2017). Selected specimens were imaged using a Scanning Electron
145   Microscope (SEM).
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150
151   Table 1. Sample information including the geographical position, water depth, habitat
152   type, in addition to the abundance and raw species richness of ostracod assemblages.

Location	Island	Depth (m)	Longitude	Latitude	Species richness	Abundance	Habitat
Haramu Passage	Pemba	20	39.6280	-5.0946	37	69	fore reef
Haramu Passage	Pemba	30	39.6280	-5.0946	35	60	fore reef
Kokota Reef	Pemba	25	39.6472	-5.1311	64	235	fringing reef
Kokota Reef	Pemba	16	39.6472	-5.1311	78	364	fringing reef
Mapenduzi wall	Pemba	40	39.6026	-5.2334	60	235	fore reef
Mapenduzi wall	Pemba	42	39.6026	-5.2334	55	188	fore reef
Misali Island	Pemba	20	39.5918	-5.2456	65	254	fore reef
Ras Nungwi peak	Zanzibar	12	39.3192	-5.7225	56	296	fringing reef
Ras Nungwi peak	Zanzibar	12-14	39.3192	-5.7225	46	116	fringing reef
Ras Nungwi peak	Zanzibar	20	39.3192	-5.7225	81	311	fringing reef

Ras Nungwi	Zanzibar	16	39.3425	-5.7481	92	408	fringing reef
Ras Nungwi	Zanzibar	20	39.3425	-5.7481	37	76	fringing reef
Mnemba Atoll	Zanzibar	30	39.3939	-5.8489	33	87	sand flat
Ocean Paradise	Zanzibar	3	39.3642	-5.9183	46	231	back reef
Bawe Island	Zanzibar	9-30	39.1408	-6.135	80	410	fringing reef
Bawe Island	Zanzibar	9-30	39.1408	-6.135	64	308	fringing reef
Stone Town	Zanzibar	12	39.1474	-6.2137	77	519	fringing reef
Stone Town	Zanzibar	20	39.1474	-6.2137	66	361	fringing reef
Menai Bay	Zanzibar	1	39.3719	-6.3236	36	241	mangrove
Kizimkazi Beach	Zanzibar	10	39.46	-6.4381	24	59	sand flat
Mafia outside	Mafia	21	39.828	-7.9179	44	94	fore reef
Mafia outside	Mafia	20	39.8224	-7.9221	82	347	fore reef
Chole Bay 1	Mafia	18-21	39.8173	-7.9414	27	74	backreef
Chole Bay 2	Mafia	15-18	39.7871	-7.9483	77	241	fringing reef
Chole Bay 2	Mafia	20	39.786	-7.9491	72	281	fringing reef
Mafia Lodge	Mafia	0-3	39.7479	-7.9734	62	397	fringing reef

153

154   3.2 Quantitative analysis

155   We used Hill numbers (i.e., the effective number of equally abundant species)

156   parameterized by a diversity order q to estimate ostracod diversity in each sample and

157   island (Hill, 1973). Hill numbers have several major advantages over other diversity

158   indices and are increasingly adopted by ecologists (Chao et al., 2020). For example, the

159   Hill numbers will double when combining two identically distributed but distinct

160   communities, so they obey the "doubling property" and behave like species richness

161   (Chao et al., 2014b). In other words, the unit of Hill numbers is also "species" and thus

162   is more ecologically meaningful than other traditional diversity indices. Also, the order

163   q of the Hill numbers controls the sensitivity of the diversity metric to species relative

164   abundance. When the order $q=0$, Hill number (^0D) reduces to species richness; when

165   the order $q=1$, Hill number (^1D) measures the diversity of the abundant species; when

166   the order $q=2$, Hill number (^2D) measures the diversity of dominant species (Chao et

167   al., 2014b). Therefore, besides species richness, the Hill numbers also estimate the

168   effective (or hypothetical) numbers of abundant and dominant species. Coincidentally,

169   the Hill numbers ^1D and ^2D are equivalent to the exponential of Shannon entropy and

170   Simpson index (hereafter referred to as Shannon and Simpson diversity), respectively

171   (Chao et al., 2014b), making them conceptually easy to understand by ecologists. To

172   make a fair comparison among multiple assemblages, we standardized the Hill numbers

173   with rarefaction or extrapolation to the largest sample completeness possible across

174   samples (82.5%) and across islands (98.6%) (Chao et al., 2020). The standard error and

175   95% confidence intervals of the Hill numbers were estimated by bootstrap resampling,

176   which was repeated 1000 times. Species evenness, $^{q}E_3(p) = (^{q}D - 1)/(S - 1)$, where ^{q}D

177   denotes Hill numbers of order q, and S denotes species richness, was quantified using

178   the continuous profiles of Hill numbers as functions of order q (Chao and Ricotta, 2019).

179   A gradual profile suggests a more even community in which the species richness and

180   number of abundant and dominant species are similar. In contrast, a steep profile

181   indicates an uneven community comprised of one or a few dominant species (Mamo et

182   al., 2023).

183

184   To distinguish biofacies associated with different benthic habitats, we conducted

185   hierarchical cluster analysis based on Ward's minimum variance and three Hill number-

186   based dissimilarity indices, including Sørensen (q=0), Horn (q=1), and Morisita-Horn

187   (q=2), to estimate the effective proportion of un-shared species in the ostracod

188   assemblages (Chao et al., 2014a). Similarly, the order q controls the sensitivity of the

189   Hill number-based dissimilarities to species relative abundance. While the classic

190   Sørensen dissimilarity is presence-absence based, the latter two indices are designed to

191   quantify the compositional dissimilarities of abundant and dominant species,

192   respectively. The Ward's algorithm is preferred for delineating biofacies because it

193   minimizes the error sum of squares within clusters and generates more balanced clusters.

194   The number of clusters was determined by considering both the structure of the

195   dendrograms and the average silhouette width, with a higher value indicating greater

196   cohesion and separation of clusters. We also performed a non-Metric Multidimensional

197   Scaling (nMDS) to visualize and summarize faunal similarities among ostracod

198   assemblages in two-dimensional space. Stress values were calculated to quantitatively

199   weigh the 'goodness of fit' between the original input data matrix and the ultrametric

200   matrix of the resultant nMDS scatter plots (Hong et al., 2022; Kruskal, 1964). We used

201   a compositional heat map to illustrate the relationships between samples by Horn

202   dissimilarities and between species by Hellenger distances.

203

204   All analyses were implemented in RStudio. We used the package 'iNEXT' to estimate

205   diversity (Chao et al., 2014a; Hsieh et al., 2016) and 'vegan' for our multivariate

206   analyses (Oksanen et al., 2020). Figures and maps were constructed using 'ggplot2'
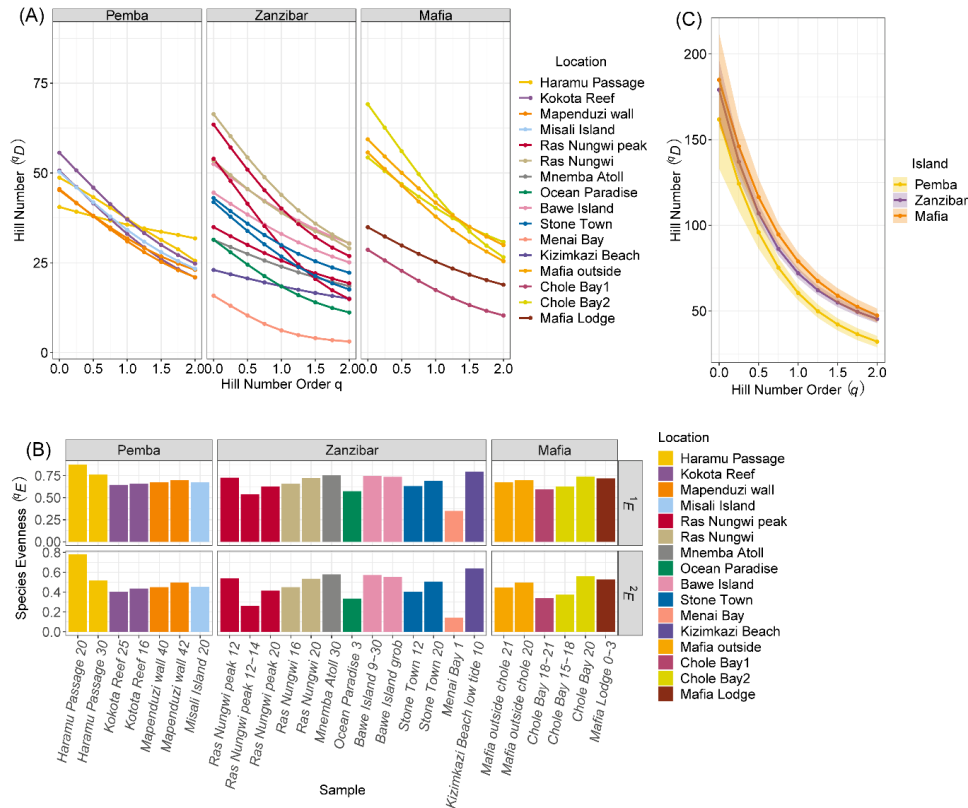
207   (Wickham, 2020).

208

209   **4 Results**

210   4. 1 Diversity

211   A total of 6262 ostracods were recovered from 26 samples at 16 locations around the

212   Zanzibar Archipelago. They represent remarkably diverse ostracod assemblages

213   comprised of 235 species under 77 genera. Considering the alpha diversity of individual

214   sample as measured by Hill number of different order q, the spatial diversity patterns

215   were relatively consistent for rare (i.e., species richness, ^{0}D) and abundant (^{1}D) species.

216   The highest values were recorded for fringing reefs at Chole Bay 2 and Ras Nungwi,

217   followed by fringing reefs at Mafia outside and Ras Nungwi peak (Figs. 2A, 3, S1-S2).

218   Moderately high levels of diversity were observed at fore reef sites in Pemba Island and

219   fringing reefs at Bawe, Stone Town, and Mafia Lodge. In terms of the diversity of

220   dominant (^{2}D) species, there was a more homogenous distribution with similarly high

221   values found at various fringing and fore reefs, including Chole Bay 2, Mafia outside,

222   Haramu Passage, Bawe Island, Ras Nungwi and Ras Nungwi peak. All remaining

223   localities (Chole Bay 1, Mnemba Atoll, Ocean Paradise and Kizimkazi Beach)

224   characterized by sand flat and back reef habitats had consistently low diversity across

225   all order q, especially Menai Bay that was lined with mangrove stands. Evenness was

226   highest at Haramu Passage and lowest at Menai Bay for both orders $q=1$ and $q=2$ (Figs.

227   2B, S3). With respect to the gamma diversity of each island, Mafia and Zanzibar were

228   almost equally diverse across all order q, while Pemba had significantly lower diversity

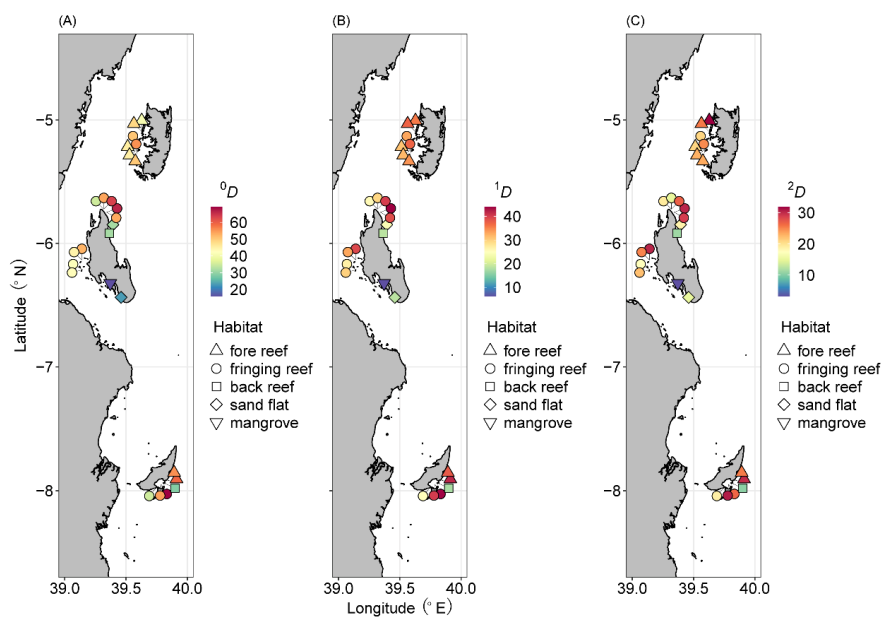229   for abundant and dominant species (Figs. 2C, S4).

230

231

Fig. 2. Diversity results of Zanzibar Archipelago ostracods. (A) Alpha diversity of each sample shown by Hill number profile based on 82.5% sample coverage. The overall elevation of the profile indicates the diversity based on hill number across different order q. The levelness of the line indicates species evenness of the assemblage, because a complete leveled diversity profile would suggest that the numbers of total, common and dominant species are all the same. (B) Evenness of each sample as the normalized slope of Hill number profile for order $q=1$ and $q=2$ based on 82.5% sample coverage. (C) Gamma diversity of each island shown by Hill number profile based on 98.6% sample coverage. The shade area shows 95% confidence interval of the profile.

241

Fig. 3. Diversity maps of Zanzibar archipelago ostracod. Distributions of Hill numbers ^{0}D (A: $q = 0$, species richness), ^{1}D (B: $q = 1$, exponential Shannon), and ^{2}D (C: $q = 2$, inversed Simpson). We used 82.5% sample coverage to standardize the Hill number estimates. Diversity and habitat are represented by color and shape as in the legends, respectively.

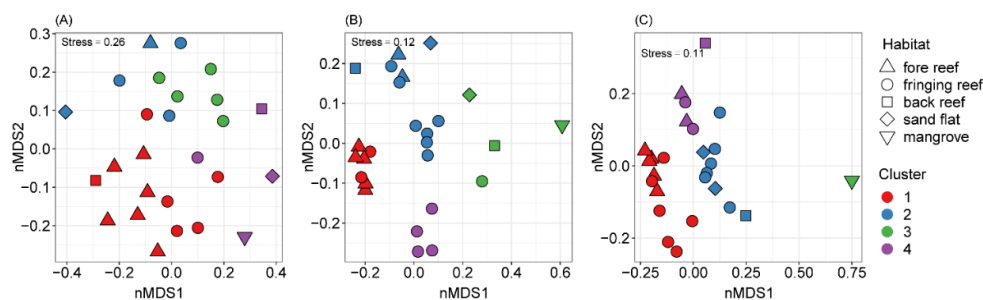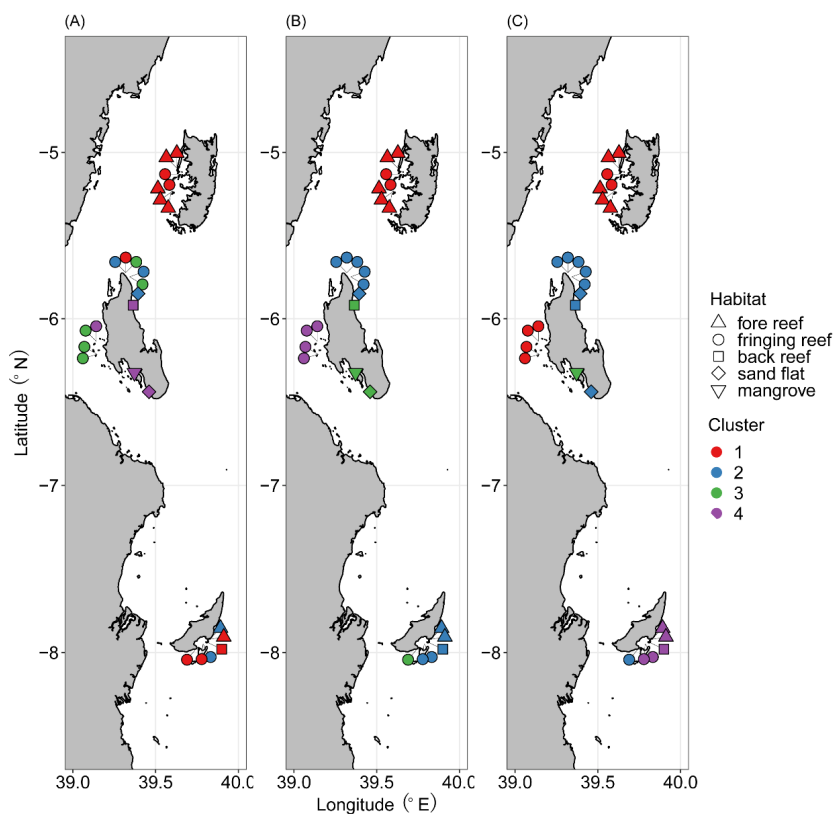4.2 Multivariate analysis

First, cluster analyses based on Sørensen, Horn, and Morisita-Horn dissimilarities delineated biofacies considering faunal composition in terms of species occurrence, relative abundance of abundant species, and relative abundance of dominant species, respectively. The greatest average silhouette width suggested the division of samples into ten clusters for all three dissimilarity measures; however, it is beyond interpretable to have too many clusters, given the size of our dataset. We, therefore, referred to the structure of the dendrograms based on three dissimilarity measures to determine the optimum number of clusters to be four (Fig. S5). The NMDS results showed a clear separation of four biofacies based on Horn and Morisita-Horn dissimilarities, but not Sørensen dissimilarity, which was calculated with a relatively high stress value (0.26) (Fig. 4). Ostracod faunas in Pemba Island constituted a distinct group across all levels of faunal composition from presence/absence to relative abundance (Biofacies 1; Fig.

11

262 5). Ras Nungwi, Ras Nungwi peak, and nearby Menemba Atoll were congregated with
263 different sites around Zanzibar and Mafia in Biofacies 2, including Mafia outside and
264 Chole Bay 2 in Sørensen, Mafia outside, Chole Bay 1 and Chole Bay 2 in Horn, Ocean
265 Paradise, Kizimkazi Beach and Mafia Lodge in Morisita-Horn analysis (Fig. 5).
266 Samples assigned to Biofacies 3 and 4 strongly varied depending on the dissimilarity
267 matrix used, indicating these biofacies have different ecological meaning among three
268 cluster analyses. Specifically, they scattered around the entire Zanzibar Island based on
269 Sørensen dissimilarity. Biofacies 4 was distributed along the western coast of Zanzibar,
270 including Stone Town and Bawe, and Biofacies 3 covered the remaining Zanzibar
271 locations (Menai Bay, Ocean Paradise and Kizimkazi Beach) in addition to Mafia
272 Lodge based on Horn dissimilarity. On the other hand, when Morisita-Horn
273 dissimilarity was applied, Menai Bay was different from all other sites as a distinctive
274 Biofacies 3 while most Mafia sites (Mafia outside, Chole Bay 1, and Chole Bay 2)
275 aggregated in Biofacies 4. Considering the performance of multivariate analyses to
276 reflect and interpret biological patterns, we think that cluster and NMDS results based
277 on Horn dissimilarity most reasonably captured the underlying ecological significance
278 of reefal versus non-reefal facies as determined by benthic community, depth, and
279 possibly anthropogenic disturbances (see the Discussion section). We therefore focus
280 on the four biofacies as divided by Horn-based analysis to scrutinize their diversity and
281 compositional structure in relation to a set of environmental variables.
282

284 Fig. 4. nMDS ordinations showing biofacies based on (A) Søensen, (B) Horn, and (C)
285 Morisita-Horn dissimilarities and Ward's minimum variance cluster analysis. Cluster
286 and habitat are represented by color and shape as in the legends, respectively. Note that
287 the color schemes are independent among panels; thus, the biofacies based on different
288 dissimilarities are not necessarily related.

Fig. 5. Distribution of ostracod Biofacies 1-4 based on (A) Søensen, (B) Horn, and (C) Morisita-Horn dissimilarities and Ward's minimum variance cluster analysis. Note that the color schemes are independent among panels; thus, the biofacies based on different dissimilarities are unrelated. Cluster and habitat are represented by color and shape as in the legends, respectively.

Each biofacies based on Horn dissimilarity index was demonstrated with the top 10 species of highest mean relative abundance as shown in Table 2 and Figures 6-8. Noticeably, the Pemba fauna in Biofacies 1 was dominated by genus *Neonesidea* (*N.* cf. *crepidula* and *N. schulzi*) and *Bosasella* (*B. profunda* and *B. elongate*), together with *Paracytheridea tschoppi* (Fig. 9; Table 2). Biofacies 2 included the most diverse sites in Zanzibar and Mafia, which all shared similar faunal structures with a high abundance of *Loxocorniculum* sp. 2, *Xestoleberis rotunda*, *Paracytheridea albatros* and *Loxoconcha* sp. 3. Biofacies 3 composed of low-diversity sites in Zanzibar and Mafia was distinguished by highly abundant *Perissocytheridea* sp.1, *Xestoleberis hanaii*, as
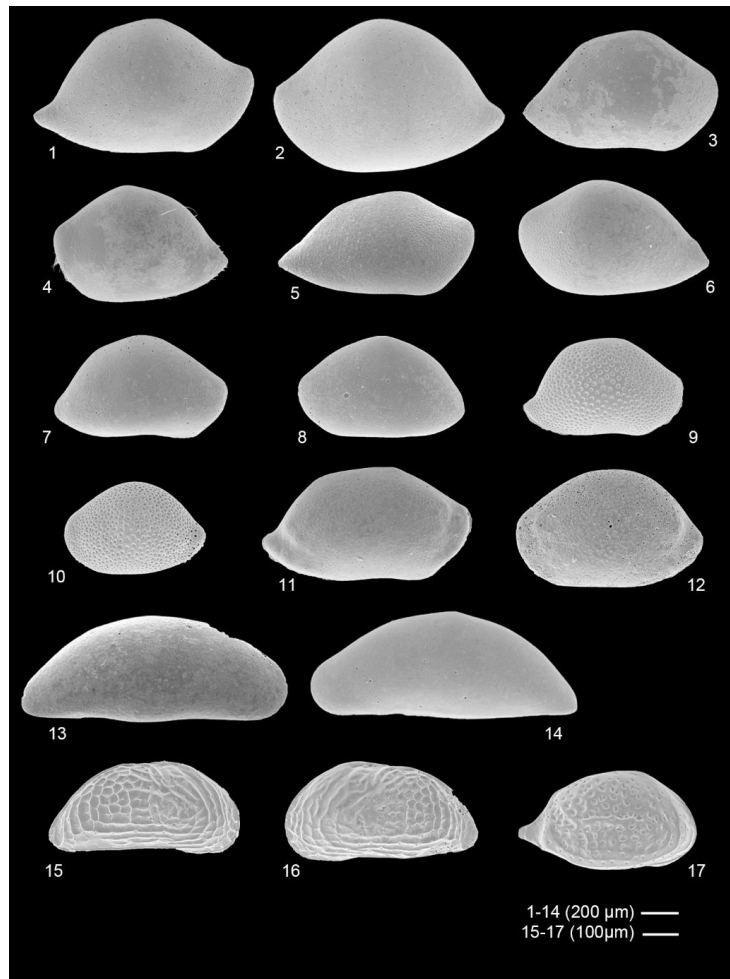
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305   well as three *Loxoconcha* species (*L.* sp. 3, *L. ghardaqensis* and *L. lilljeborgii*). Finally,

306   the faunal structure of Biofacies 4 in western Zanzibar showed some similarities to that

307   of Biofacies 1 in Pemba with many common species, however, they clearly differed by

308   the dominance of *Xestoleberis hanaii* and *Patrizia nucleuspersici* in Biofacies 4.
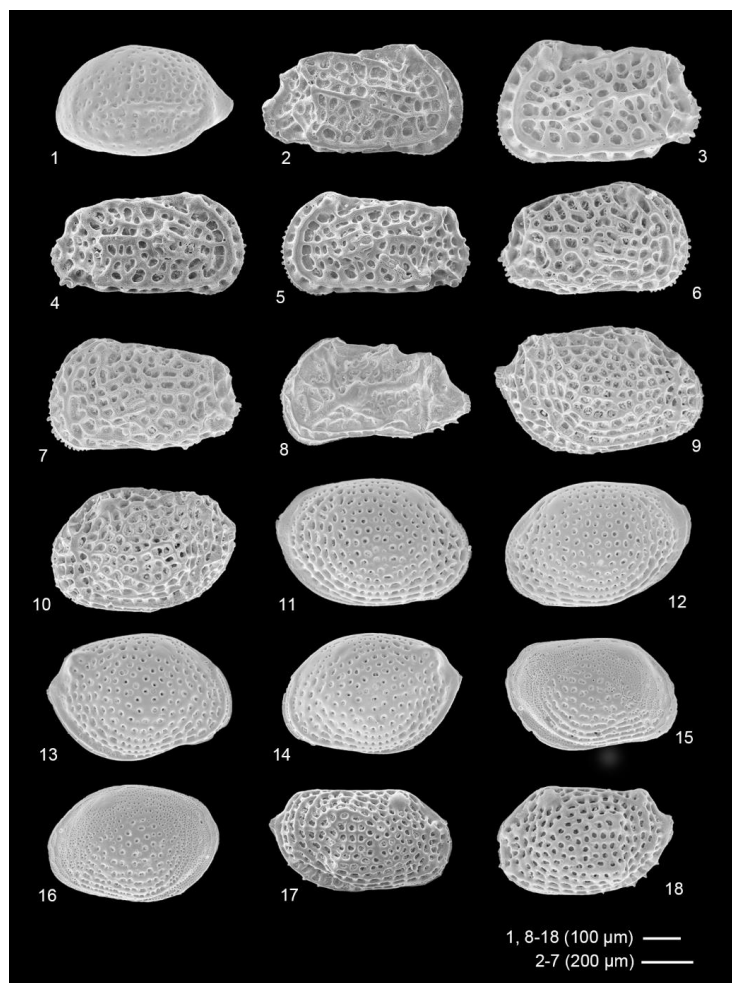
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310   Table 2. List of top 10 species of highest % mean relative abundance for Biofacies 1-4

311   based on Horn dissimilarity.

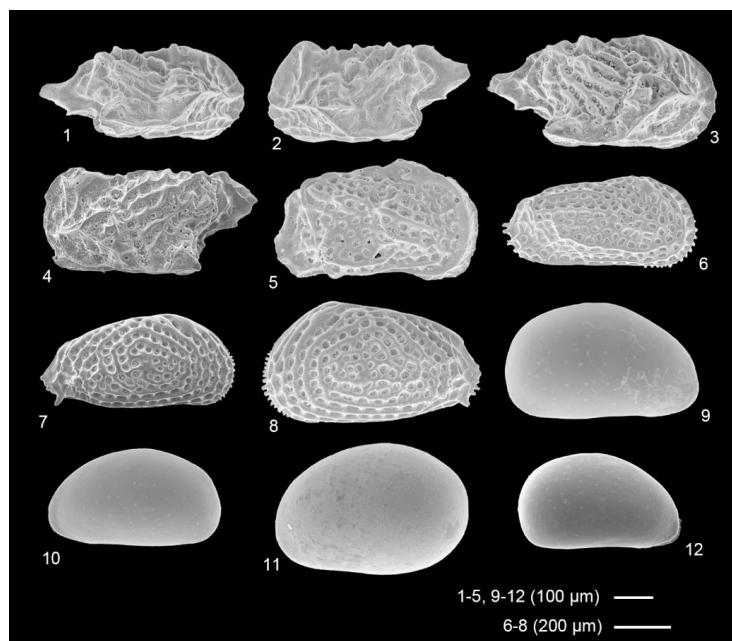| Species	Biofacies1	Biofacies2	Biofacies3	Biofacies4
Neonesidea cf. *crepidula*	0.085857	NA	NA	NA
Bosasella profunda	0.079436	NA	NA	0.040846
Neonesidea schulzi	0.075285	0.032551	0.024322	0.041291
Paracytheridea tschoppi	0.035779	NA	NA	0.028826
Loxocorniculum sp. 2	0.030562	0.063399	NA	NA
Xestoleberis hanaii	0.028593	0.039954	0.084378	0.071834
Patrizia nucleuspersici	0.02842	NA	NA	0.057965
Paranesidea cf. *spongicola*	0.026203	NA	NA	0.029754
Xestoleberis sp. 1	0.023801	NA	NA	NA
Bosasella elongata	0.023369	NA	0.017579	NA
Xestoleberis rotunda	NA	0.061861	NA	NA
Paracytheridea albatros	NA	0.045056	0.037464	NA
Loxoconcha sp. 3	NA	0.041327	0.110386	NA
Bosasella sp. 1	NA	0.040122	NA	NA
Macrocyprina maddocksae	NA	0.039264	NA	NA
Caudites exmouthensis	NA	0.027832	NA	NA
Paranesidea sp. 1	NA	0.025497	NA	NA
Perissocytheridea sp.1	NA	NA	0.157932	NA
Loxoconcha ghardaqensis	NA	NA	0.073153	NA
Hiltermannicythere rubrimaris	NA	NA	0.04805	NA
Loxoconcha lilljeborgii	NA	NA	0.033061	NA
Neohornibrookella lactea	NA	NA	0.018616	NA
Neonesidea sp. 3	NA	NA	NA	0.048331
Neonesidea paiki	NA	NA	NA	0.042016
Loxoconcha cf. *gisellae*	NA	NA	NA	0.035319
Perissocytheridea? sp. 2	NA	NA	NA	0.029391

312

Fig. 6. Scanning electron microscopy images of the top 10 ostracod species of highest % mean relative abundance for Biofacies 1-4 based on Horn dissimilarity. 1, *Neonesidea* cf. *crepidula*, RV; 2, *Neonesidea* cf. *crepidula*, LV; 3, *Neonesidea paiki*, RV; 4, *Neonesidea paiki*, LV; 5, *Neonesidea schulzi*, RV; 6, *Neonesidea schulzi*, LV; 7, *Neonesidea* sp. 3, RV; 8, *Neonesidea* sp. 3, LV; 9, *Paranesidea* cf. *spongicola*, RV; 10, *Paranesidea* cf. *spongicola*, LV; 11, *Paranesidea* sp. 1, RV; 12, *Paranesidea* sp. 1, LV; 13, *Macrocyprina maddocksae*, RV; 14, *Macrocyprina maddocksae*, LV; 15, *Perissocytheridea* sp.1, RV; 16, *Perissocytheridea* sp.1, LV; 17, *Perissocytheridea*? sp. 2, RV. All adults and lateral views.

Fig. 7. Scanning electron microscopy images of the top 10 ostracod species of highest % mean relative abundance for Biofacies 1-4 based on Horn dissimilarity. 1, *Perissocytheridea*? sp. 2, LV; 2, *Bosasella elongate*, RV; 3, *Bosasella elongate*, LV; 4, *Bosasella profunda*, RV; 5, *Bosasella profunda*, LV; 6, *Bosasella* sp. 1, RV; 7, *Bosasella* sp. 1, LV; 8, *Caudites exmouthensis*, LV; 9, *Loxoconcha ghardaqensis*, RV; 10, *Loxoconcha ghardaqensis*, LV; 11, *Loxoconcha* cf. *gisellae*, RV; 12, *Loxoconcha* cf. *gisellae*, LV; 13, *Loxoconcha lilljeborgii*, RV; 14, *Loxoconcha lilljeborgii*, LV; 15, *Loxoconcha* sp. 3, RV; 16, *Loxoconcha* sp. 3, LV; 17, *Loxocorniculum* sp. 2, RV; 18, *Loxocorniculum* sp. 2, LV. All adults and lateral views.
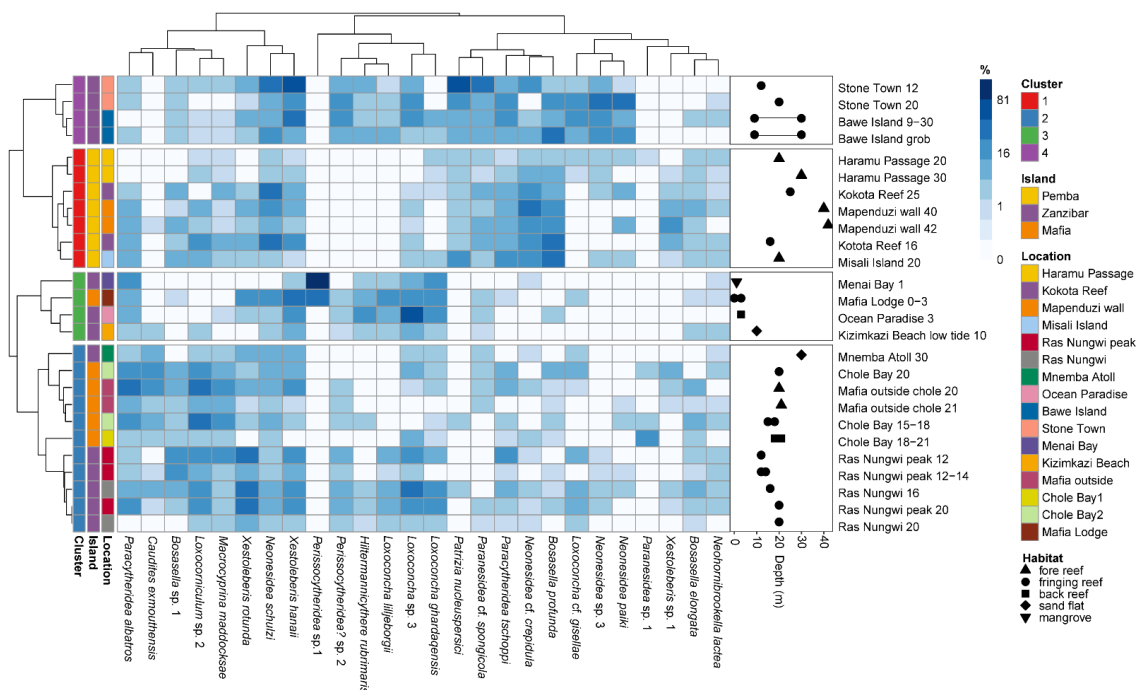
Fig. 8. Scanning electron microscopy images of the top 10 ostracod species of highest % mean relative abundance for Biofacies 1-4 based on Horn dissimilarity. 1, *Paracytheridea albatross*, RV; 2, *Paracytheridea albatross*, LV; 3, *Paracytheridea tschoppi*, RV; 4, *Paracytheridea tschoppi*, LV; 5, *Neohornibrookella lactea*, RV; 6, *Hiltermannicythere rubrimaris*, RV; 7, *Patrizia nucleuspersici*, RV; 8, *Patrizia nucleuspersici*, LV; 9, *Xestoleberis hanaii*, RV; 10, *Xestoleberis hanaii*, LV; 11, *Xestoleberis rotunda*, LV; 12, *Xestoleberis* sp. 1, RV. All adults and lateral views.

Fig. 9. Dendrograms based on Horn dissimilarity between samples and Hellenger distances between top 10 species of highest mean relative abundance in each cluster. The blue heatmap indicates the relative (%) abundance of each species in each sample. The side panel shows water depth and habitat type of each sample (note that several samples are shown by their corresponding depth ranges).

5 Discussion

Through Hill number profile and multivariate analyses, we quantified a highly diverse ostracod fauna in the Zanzibar Archipelago composed of four distinct biofacies. The delineation of biofacies varied considerably depending on the dissimilarity matrix used, indicating inconsistent faunal structures across different levels of species information from occurrence to relative abundance (Fig. 5). In terms of the presence/absence of species (Sørensen dissimilarity), all Pemba sites united in Biofacies 1 but the assignment of Zanzibar and Mafia sites into Biofacies 1-4 seemingly conformed to a noisy pattern. Accordingly, four biofacies intersected with each other in nMDS space with relatively high stress value (Fig. 4A). A possible explanation is that the occurrence of individual species may be homogenous among sites in similar environmental

362   conditions within a finite geographic region. Many species are likely to be ubiquitous
363   across the entire neritic zone despite showing certain ecological preferences, and the
364   redeposition processes may further facilitate the mixing of death assemblages to blur
365   the spatial signal at a local scale (Frenzel and Boomer, 2005). Consequently, species
366   presence in all available habitats may translate to considerable faunal similarities
367   among biofacies as measured by Sørensen index. When considering the composition of
368   abundant species (Horn dissimilarity) (Figs. 4B and 5B), the identification of four
369   biofacies instead reflected significant changes in ostracod assemblages along two
370   important environmental gradients, which are benthic community type and water depth.
371   Specifically, Biofacies 1 and 2 characterize typical fore reefs in deep subtidal (sampling
372   depth 16-42 m) and fringing reefs in shallow subtidal (12-30 m), respectively (Fig. 9).
373   Biofacies 3 indicates intertidal habitats with plant cover (0-10 m), and finally Biofacies
374   4 features degraded fringing reefs in shallow subtidal (9-30 m) (see discussion below).

375

376   We summarized the ecological preferences of dominant genera in each biofacies based
377   on Horn dissimilarity (Table 3 and Fig. 9) and investigated how key environmental
378   factors (benthic community type, water depth, and anthropogenic disturbance) may
379   control the distribution and diversity of reefal ostracod assemblages. First of all,
380   *Neonesidea* and *Paranesidea* (family Bairdiidae) are typical reefal genera that reach
381   their maximum diversity and incidence on reefs and reef-associated habitats in tropical
382   shallow-marine environments (Whatley and Watson, 1988; Maddocks, 2013; Titterton
383   and Whatley, 1988). Their dominance in Biofacies 1 is consistent with our background
384   understanding that the Pemba reefs were pristine and healthy (Ussi et al., 2019;
385   Grimsditch et al., 2009). However, it should be noted that individual species of these
386   genera likely have different environmental tolerance. For example, *N.* cf. *crepidula*
387   were restricted to Biofacies 1 while *N. schulzi* were widespread among four biofacies
388   inhabiting both reef and algae habitats (Fig. 9) (Mostafawi et al., 2005). *Bosasella* as
389   another prominent component of Biofacies 1 is also known to occur on coral reefs in
390   the western Indian Ocean (Munef et al., 2012; Jellinek, 1993). *Paracytheridea* and
391   *Caudites* on the other hand are loosely categorized as reefal genera, as their dominance
392   on coral reefs was reported but not studied in detail (Whatley and Watson, 1988; Keyser
393   and Mohammed, 2021). In this study, they were common on fore- and fringing-reefs in
394   Biofacies 1 and 2 (Fig. 9). *Loxoconcha* and *Loxocorniculum* (family Loxoconchidae)
395   as two phylogenetically related and ecologically similar genera exhibited ubiquitous

396   distribution around Zanzibar Archipelago with highest relative abundance in Biofacies

397   3 followed by Biofacies 2. As generalists, they thrive on a wide variety of benthic

398   habitats across the neritic zone and show affinities to plant substrates (algae and

399   seagrass beds) in particular (Munef et al., 2012; Keyser and Mohammed, 2021; Kamiya,

400   1988). The ecology of *Xestoleberis* is very similar to that of Loxoconchidae, living both

401   on coral reefs and algal flats (Keyser and Mohammed, 2021; Munef et al., 2012;

402   Whatley and Watson, 1988; Kamiya, 1988). This genus was almost equally weighted

403   in all biofacies, although individual species clearly preferred different environments, as

404   *X. hanaii* prevailed in Biofacies 3 and 4 while *X. rotunda* only in Biofacies 2 (Fig. 9).

405   *Patrizia* is documented as a reefal genus in lower littoral zone along the eastern coast

406   of tropical Africa (Jellinek, 1993). It dominated the relatively deep fringing-reef faunas

407   of Biofacies 4, which were subject to sewage-derived nutrient and trace metal pollution

408   from the Zanzibar Town (Narayan et al., 2022; Bravo et al., 2021). Different from all

409   the above-discussed genera, *Hiltermannicythere* and *Perissocytheridea* are restricted to

410   shallow intertidal environments as phytal and sediment-dwelling taxa, respectively

411   (Jellinek, 1993), which explains their abundance in our Biofacies 3. *Perissocytheridea*

412   is especially considered a bioindicator of brackish water facies (Nogueira and Ramos,

413   2016; Keyser, 1977). Furthermore, we revealed a more generalized pattern of the

414   compositional differences among biofacies with the top 5 families of highest mean

415   relative abundance in each biofacies (Fig. 10).

416

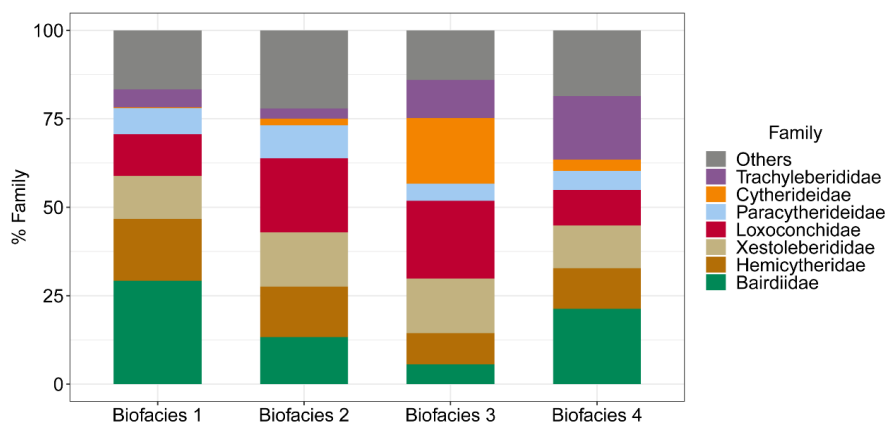417   Table 3. Autoecology summary of important ostracod genera.

Genus	Predominant habitats	References
Neonesidea	Coral reef	Whatley and Watson (1988); Maddocks (2013); Titterton and Whatley (1988); Maddocks (1969)
Paranesidea	Coral reef	Titterton and Whatley (1988); Whatley and Watson (1988); Maddocks (1969)
Bosasella	Coral reef	Munef et al. (2012)
Loxoconcha	Algal mat and reef	Keyser and Mohammed (2021); Whatley and Watson (1988); Munef et al. (2012); Kamiya (1988)
Loxocorniculum	Algal mat and reef	Munef et al. (2012); Kamiya (1988)
Xestoleberis	Algal mat and reef	Keyser and Mohammed (2021); Whatley and Watson (1988); Munef et al. (2012); Kamiya (1988)
Patrizia	Coral reef	Jellinek (1993)

Hiltermannicythere	Intertidal algal mat	Jellinek (1993); Keyser and Mohammed (2021)
Paracytheridea	Coral reef	Whatley and Watson (1988)
Caudites	Coral reef	Whatley and Watson (1988); Keyser and Mohammed (2021)
Perissocytheridea	Intertidal sand flat, brackish water	Nogueira and Ramos (2016); Keyser (1977)

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420

421 Fig. 10. Family composition of Biofacies 1-4 based on Horn dissimilarity. The top 5
422 families of the highest % relative abundance in each biofacies are shown.

423

424 Thus, the distribution of shallow-marine ostracods in the Zanzibar Archipelago is
425 characterized by three reefal facies and one intertidal facies. Yet slight differences in
426 bathymetry, benthic community type, and anthropogenic impacts likely contributed to
427 subtle faunal changes among the reefal Biofacies 1, 2, and 4. The fore reefs in Pemba
428 (Biofacies 1) were deepest with high incidence and diversity of live hard corals
429 (Gavrilets and Losos, 2009; Ussi et al., 2019), which accounted for the definite
430 dominance of ostracod reefal taxa (Bairdiidae and *Bosasella*) over algal taxa
431 (Loxoconchidae and Xestoleberididae) (Figs. 9-10). Moderately high levels of diversity
432 in terms of rare, abundant, and dominant species were observed for these ostracod
433 assemblages (Figs. 2-3). The Pemba reefs are thereby considered the most mature and
434 authentic reef ecosystem, serving as a natural reference for comparing with other sites.
435 The fringing-reef fauna of western Zanzibar (Stone Town and Bawe, Biofacies 4)
436 exhibited certain similarities with the Pemba fauna as indicated by the prevalence of
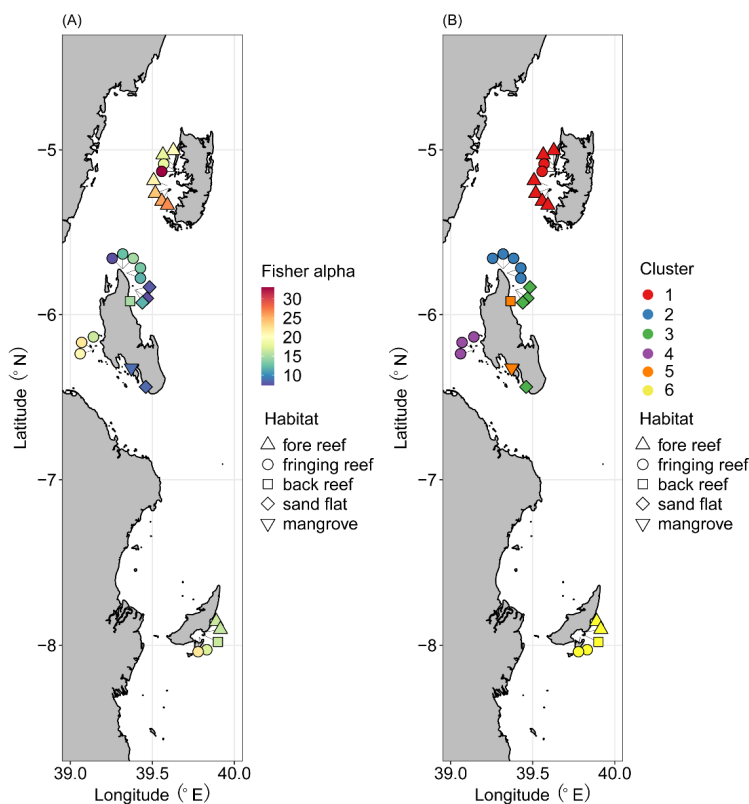
437 *Bosasella profunda*, *Paracytheridea tschoppi*, and *Paranesidea* cf. *spongicola* in both
438 facies (Fig. 9). Indeed, they were grouped together based on the composition of
439 dominant species (Morisita-Horn analysis) (Fig. 5C). Faunal similarities between
440 Pemba and Stone Town make sense as they are in comparable baseline conditions of
441 water depths and hydrology along the protected western coast of Zanzibar Archipelago,
442 in contrast to Ras Nungwi and Chole Bay that are exposed to oceanic disturbances from
443 the east (Fig. 1). However, Biofacies 4 was differentiated from Biofacies 1 by the
444 dominance of *Patrizia* in conjunction with the absence of *Neonesidea* cf. *crepidula*. It
445 also had the highest relative abundance of Trachyleberididae genera among all facies
446 (Fig. 10), for example, *Adencythere*, *Strobilocythere, Bradyon,* and *Actinocythereis*, but
447 their ecologies are not well understood. Stressful environmental conditions in terms of
448 overexploitation, tourism and coastal pollution offer the most possible explanation for
449 such a unique faunal composition and comparatively low diversity of Biofacies 4 (Figs.
450 2-3) (Bravo et al., 2021; Larsen et al., 2023). Consistently, foraminifera and coral
451 surveys indicated early stages of reef degradation there (Narayan et al., 2022; Bravo et
452 al., 2021; Thissen and Langer, 2017) It is possible that ongoing anthropogenic
453 disturbances near the Stone Town will eventually exceed the critical threshold levels to
454 cause more pronounced changes in ostracod faunal structures in terms of dominant
455 species through a shift in benthic habitat (Narayan et al., 2022; Hong et al., 2022). Other
456 than Biofacies 1 and 4, Biofacies 2 represented a different type of reefal habitat of Ras
457 Nungwi, Chole Bay, Mafia outside, and Mnemba Atoll (Fig. 5B). Algal taxa
458 (Loxoconchidae and Xestoleberididae) and reefal taxa (Bairdiidae, *Bosasella*,
459 *Paracytheridea*, and *Caudites*) reached equally high levels of relative abundance there
460 (Figs. 9-10). Most sites in Biofacies 2 were relatively shallow (12-21 m) except for
461 Mnemba Atoll (30 m), and they covered the transitional zone from intertidal sandy
462 bottom to subtidal true reefs. Microhabitats on the reef platforms of Biofacies 2 are
463 believed to be diverse and heterogenous with interlaced live and dead corals, algae and
464 seagrass, calcareous sands, as well as bare substrate rock (Ussi et al., 2019; Larsen et
465 al., 2023), which facilitated the coexistence of reefal and algal ostracods and
466 consequently the highest diversity of local assemblages (Figs. 2-3). The remaining
467 Biofacies 3 corresponded to the shallowest intertidal habitats with various benthic
468 communities, including back reef, fringing reef, sand flat, and mangrove (Fig. 5B).
469 Typical reefal taxa (Bairdiidae and *Bosasella*) dropped to their lowest relative
470 abundance in this facies, replaced by large numbers of Loxoconchidae,

22

471   *Perissocytheridea,* and *Hiltermannicythere* that well adapted to shallow euryhaline

472   conditions (Figs.9-10). Not surprisingly, the diversity of Biofacies 3 was much lower

473   than that of open-ocean reefal facies, as drastic changes in temperature, salinity,

474   dissolved oxygen, and wave energy in the intertidal zone may be too challenging for

475   many marine taxa (Figs. 2-3) (Morley and Hayward, 2007; Frenzel and Boomer, 2005).

476   The mangrove habitat at Menai Bay was unique concerning the absolute dominance of

477   *Perissocytheridea* in line with its lowest diversity and evenness (Figs. 2-3). It indeed

478   constituted an independent biofacies based on Morisita-Horn analysis (Fig. 5C).

479

480   The division scheme of four biofacies based on Horn dissimilarity explicitly revealed

481   spatial patterns of ostracod distribution in aspect of diversity and composition, as

482   discussed above. Our results are generally concordant with a previous study on benthic

483   foraminifera, which separated six clusters of Pemba, Stone Town, Mafia Bay, Ras

484   Nungwi, Mnemba Atoll, and Menai Bay, respectively (Fig. 11B) (Thissen and Langer,

485   2017). Each of these foraminifera clusters corresponded to major habitat types, as

486   argued by the authors (Thissen and Langer, 2017), and we accordingly pointed out the

487   consistent role of habitat factors in shaping the biogeography of both ostracod and

488   foraminifera biotas. However, the diversity patterns of these two groups were

489   apparently different among reefal habitats (Figs. 3, 11A). High, moderate, and low

490   levels of diversity were recorded on fore reefs (Pemba), fringing reefs (Mafia and

491   Zanzibar), and intertidal (Zanzibar) for foraminifera, in contrast to fringing reefs (Mafia

492   and Zanzibar), fore reefs (Pemba), and intertidal (Zanzibar) for ostracods, respectively.

493   Such discrepancies may imply a tight association of foraminifera with reef ecosystem

494   and their ultra-sensitivity to reef health, since their diversity generally decreased from

495   pristine, mature reefs to degraded, marginal reefs. Ostracods, on the other hand, may

496   be less confined or specific to reef habitats. The occupation of coral and algae substrate

497   by distinct faunal groups allows them to thrive in the transitional zone between marginal

498   and true reefs.

Fig. 11. Distributions of benthic foraminifera (A) diversity measured as Fisher alpha index; (B) cluster groups based on Q-mode cluster analysis. Modified from Thissen and Langer (2017). Diversity/cluster and habitat are represented by color and shape as in the legends, respectively.

Most importantly, this study established a clear benthic community axis along which the composition and diversity of ostracod assemblage vary, i.e., from coral reefs to algae turfs. We identified typical reefal association (Bairdiidae-*Bosasella*) versus algal association (Loxoconchidae-Xestoleberididae) (Fig. 10), and their relative dominance may be used as a direct indication of benthic community type. As there is a growing interest to monitor the degradation of reef ecosystems from the coral-dominated phase to the algae-dominated phase (Roth et al., 2018; Knowlton and Jackson, 2008; Knowlton, 2012), our finding is of potential conservation value. Ostracod species diversity was higher on shallow fringing reefs than on deep fore reefs, as the former ecosystem harbored evenly weighted reefal and algal taxa within a dynamic mosaic of

515   microhabitats. Our results thus strongly indicate the importance of coral reefs in

516   harboring conspicuously high levels of meiobenthic biodiversity, likely through finer

517   niche partitioning (Kohn et al., 1997; Fox and Bellwood, 2013). Along with the benthic

518   community factor, we quantified prominent changes in faunal structure and diversity

519   along a depth gradient, as the intertidal euryhaline assemblages transited to subtidal

520   fully marine assemblages. It is widely recognized that shallow-marine biotas are

521   especially susceptible to depth associated changes, such as temperature, salinity, wave

522   action, and light penetration (Carvalho et al., 2012; Tian et al., 2022). This study

523   showed that a narrow depth zone across the intertidal and subtidal (~40 m) was further

524   divided and occupied by distinct biofacies. Such a finely tuned vertical gradient of

525   diversity and faunal composition added to an exceedingly large regional species pool

526   (235 species) in this tropical shallow-marine setting. Last but not least, it should be

527   aware that the effects of depth and benthic community type are often intertwined with

528   each other in determining ostracod assemblages, as the habitat-building corals and algae

529   essentially exhibit depth distributions. At a regional scale like the Zanzibar Archipelago,

530   the combined effects of water depth and benthic community characteristics should be

531   considered in studying the spatial patterns of benthic organisms.

532

533   **6 Conclusion**

534   In conclusion, this study showed that the diversity and faunal composition of reefal

535   ostracod assemblages vary along benthic community and bathymetric gradients, which

536   may also be altered by local anthropogenic disturbances. Ostracod faunas on shallow

537   fringing reefs were especially diverse, which may be explained by high levels of habitat

538   complexity and heterogeneity. The relative dominance of reefal taxa (Bairdiidae)

539   versus algal taxa (Loxoconchidae-Xestoleberididae) is likely determined by the

540   proportion of coral versus algae cover on the reef platforms, though more extensive

541   studies beyond this region are needed to confirm the universality of this pattern. Coral

542   reefs worldwide are vulnerable to ongoing climate changes and other human impacts at

543   local to global scales, and many reefal species are at risk of extinction. It is of great

544   importance that we inspect and understand the immense biodiversity of meiobenthos

545   on coral reefs as an indispensable part of the ecosystem.

546

547   **Data availability**

548 Ostracod census data will be deposited into The Paleobiology Database. DOI will be

549 added later.

550

551 **Author contributions**

552 Each named author has participated sufficiently in the work to take public responsibility

553 for the content. SYT and ML developed the concept. ML collected the samples. SYT

554 carried out the experiments and collected the data. SYT and CLW performed the data

555 analyses. SYT drafted the manuscript. ML, MY, and CLW reviewed and edited the

556 manuscript.

557

558 **Competing interests**

559 The authors declare that they have no competing interests.

560

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569

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